Different or alike? Female rainbow kribs choose males of similar consistency and dissimilar level of boldness

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Different or alike? Female rainbow kribs choose males of similar consistency and dis-similar level of boldness

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Although the existence of consistent between-individual differences in behaviour ("personality differences") has been well documented during the last decade, the adaptive value of such behavioural limitations still remains an open field for researchers of animal behaviour. Personalities clearly restrict individuals in their ability to adjust their behaviour to different conditions. However, sheer costs of flexibility cannot explain the polymorphism created by personality variation. In a correlative approach, we here tested whether mate choice might act as a major driving force maintaining personality variation in the monogamous, biparental rainbow krib, *Pelvicachromis pulcher*. We personality-typed all males and females for their boldness (activity under simulated predation risk) and allowed females to choose between two males that differed in their boldness (behavioural level and consistency). Prior to the choice, females were allowed to observe both males, expressing their natural boldness towards a video animated natural predator. Both sexes showed personality differences in boldness over the short- and long-term. Furthermore, when removing side-biased females, we found a dis-assortative mating preference for the behavioural level and an assortative preference for behavioural consistency in boldness. Such preference patterns might facilitate effective parental role allocation during offspring care and/or provide genetic benefits. Our results suggest that sexual selection plays an important role in the evolution of personality differences.

Keywords: anti-predator behaviour, assortative, behavioural compatibility, cichlid, mate choice, *Pelvicachromis pulcher*, personality, risk-taking, sexual selection, side bias

Individuals have to cope with a wide array of environmental challenges. Therefore, flexibility in the expression of behavioural responses towards different and changing conditions should be favoured by selection (Sih et al., 2004). Yet, individuals often show considerable consistent between-individual differences in behaviour over time and/or contexts (Boissy, 1995). Such personality differences are common throughout the animal kingdom (reviewed in Gosling, 2001; Kralj-Fišer et al., 2014) and have been shown for various behavioural traits, such as activity pattern, aggressiveness, exploratory tendencies, boldness and fearfulness (reviewed in Dall et al., 2004; Gosling, 2001; Sih et al., 2004). Personality traits are moderately heritable (Ariyomo, Carter, et al., 2013; Patrick et al., 2013; Reif et al., 2003; van Oers et al., 2005) and have fitness consequences (e.g. Ariyomo et al., 2012; Dingemanse et al., 2005; Smith et al., 2008), suggesting they are not merely non-adaptive noise that surrounds an adaptive optimum (Wilson, 1998). Nevertheless, underlying mechanisms that generate and maintain behavioural polymorphism are largely unclear and many aspects of the growing body of theoretical frameworks still remain to be empirically tested (reviewed in e.g. Schuett et al., 2010; Wolf et al., 2010).

Recently, Schuett et al. (2010) pointed out that sexual selection may be important in generating and maintaining personality variation though this possibility has rarely been tested (but see e.g. Montiglio et al., 2016; Schuett et al., 2011). According to the proposed framework (Schuett et al., 2010), personalities are expected to play an important role in mate choice when a potential mate's behavioural phenotype is either associated with good/compatible genes that increase offspring fitness (Dingemanse et al., 2004; Ihle et al., 2015; Mays et al., 2004) or provides non-genetic benefits increasing the reproductive

63 success through parental ability and/or behavioural compatibility between mates. While
64 mate choice for genetic quality and parental ability should favour inter-individual
65 agreement in the preference for a behavioural trait, mate choice for genetic or behavioural
66 compatibility should depend on an interaction between male and female (geno- or)
67 phenotype (Schuett et al., 2010). Thus, mate choice for compatibility would lead to inter-
68 individual differences in mating preferences, creating either an assortative or dis-
69 assortative mating pattern (Schuett et al., 2010).
70
71 Not many studies to date have investigated the effect of personality traits on mate choice
72 (reviewed in Schuett et al., 2010) and some have only assessed the behaviour of the chosen
73 but not the choosing sex (Godin et al., 1996; Ophir et al., 2003). The few studies considering
74 a potential interplay between male and female personality during mate choice have often
75 found assortative mate choice for various behavioural traits, in correlative (Gonzaga et al.,
76 2010; Kralj-Fišer et al., 2013; Mascie-Taylor et al., 1988; Montiglio et al., 2016) or
77 experimental settings (Schuett et al., 2011) and an increased reproductive success of
78 assortative pairs (e.g. Ariyomo & Watt, 2013; Schuett et al., 2011). However, in studies that
79 found increased success of assortative pairs, personality data are often obtained post
80 pairing (Both et al., 2005; Harris et al., 2014; Laubu et al., 2016) not allowing to tease apart
81 whether mate choice was affected by individual personalities or whether behavioural
82 similarity was achieved post-pairing in highly successful pairs (Laubu et al., 2016). Indirect
83 evidence that dis-assortment for personality can sometimes be beneficial is provided by
84 van Oers et al. (2008), who found assortative pairs of great tits, *Parus major*, to show higher
85 rates of extra-pair paternity. Generally, positive assortment for genotypic or phenotypic

86 traits is by far more prominent in the animal kingdom than evidence for dis-assortment
87 (reviewed in Jiang et al., 2013).
88
89 Personality traits consist of two measures: the behavioural level and the degree of
90 behavioural consistency. Although there is considerable variation in within-individual
91 behavioural consistency (Dingemanse et al., 2009) the effect of such individual differences
92 in consistency on mate choice has rarely been considered (but see Schuett et al., 2011).
93 Behavioural consistency might be sexually selected for if it reflects individual quality (i.e.
94 consistency is costly under changing conditions) or if choosing a predictable (i.e. consistent)
95 mate provides reliable information about future parental care behaviour prior to mating
96 (Dall et al., 2004; Royle et al., 2010; Schuett et al., 2010). For example, a female might be
97 able to predict a male's ability to protect prospective offspring from the consistency in
98 boldness expressed prior to mate choice.
99
100 In the present study, we investigated the influence of male and female boldness (propensity
101 to engage in risky behaviour; Wilson et al., 1994) on female mate preference in a socially
102 monogamous, biparental cichlid from West Africa, the rainbow krib, *Pelvicachromis pulcher*.
103 In this species, pairs are highly territorial: they defend territories and offspring aggressively
104 against con- and heterospecifics. Therefore, we assumed individual boldness to be a trait
105 that is likely considered during mate choice. Furthermore, boldness has been shown to
106 affect foraging success (Dyer et al., 2008), egg fertilization rates (Ariyomo et al., 2012),
107 dominance (Dahlbom et al., 2011), survivorship (Smith et al., 2010), and parental care effort
108 (Budaev et al., 1999) in other fish species. We measured male and female boldness (activity

under simulated predation risk) repeatedly to test for personality differences. During mate choice experiments, females were first allowed to observe a bolder and a shyer male expressing their natural boldness towards a predator animation. Subsequent female mating preference for the two males was assessed in a standard mate choice scenario. We considered both aspects of male and female personality: the behavioural level and behavioural consistency of each individual.

We expected female preferences to depend on both, the behavioural level and behavioural consistency, with our predictions being guided by Schuett et al. (2010). For the behavioural level, we expected, that if mate choice is based on male (parental or genetic) quality, females should show a general preference for either bold or shy males (e.g. Godin et al., 1996; Kortet et al., 2012). Alternatively, if mate compatibility is more important during mate choice, females should not show an overall agreement but also consider their own personality during their choice. Because both rainbow krib parents provide offspring care we considered the second possibility, i.e. mate compatibility, to be more important for mate choice based on boldness. In species with biparental care, an assortative mating preference for certain behavioural traits could reduce sexual conflict over parental investment (Royle et al., 2010) and facilitate offspring care coordination through a better synchronisation of parental activities (Schuett et al., 2011). Depending on the environmental conditions or the biology of the species, also dis-assortative mating might sometimes have advantages (Schuett et al., 2010). For instance, species that perform several parental activities might also benefit from expressing a dis-assortative mating preference, facilitating role allocation and specialisation during offspring care. Often, a sexual dimorphism in role specialisation

can be observed with the female providing more direct offspring care and the male defending the territory (e.g. Guerra et al., 1995; Itzkowitz, 1984; Neil, 1984; Richter et al., 2010; Solomon, 1993). Nevertheless, in many species both partners can or do perform the same behaviours (see Royle et al., 2014 for a review on the flexibility of parental care behaviour), and at least partly compensate for their mates' tasks if needed (Itzkowitz, 1984; Lavery et al., 2010; Sasvari, 1986; Storey et al., 1994) indicating that sex roles might be less fixed. For the behavioural consistency, we followed up two possible mate choice scenarios: a general preference for consistent over inconsistent males, which might indicate predictability of later parental performance, and/or individual quality (Royle et al., 2010; Schuett et al., 2010) or mate choice for compatibility leading to a positive assortative preference (Schuett et al., 2011; Schuett et al., 2010).

METHODS

Ethical Note

In consideration of animal welfare, we followed the "3R" framework (Russell et al., 1959). To decrease the number of study animals needed we used predator animations instead of live predators and test males for mate choice trials were used twice. During experiments, no animals were harmed or exposed to actual predation risk. Prey fish and predators were kept separately and did not have visual contact during fish maintenance. The study was permitted by the German "Behörde für Gesundheit und Verbraucherschutz Hamburg".

155 *Study Animals and Holding Conditions*

156 Study individuals were obtained from a captive breeding stock at the University of
157 Hamburg and local suppliers. Males and females used in this study were 1 - 2 years old and
158 sexually inexperienced. Individuals were maintained in same-sex sibling groups under
159 standardised holding conditions (100 x 50 x 25 cm and 200 x 50 x 25 cm tanks, 26±1°C
160 water temperature, aerated and filtered water, weekly water changes, 12:12 hours
161 light:dark) and were fed once a day on 5 days a week with *Artemia* spec. On
162 experimentation days, fish were fed after observations. One day before the first personality
163 test, individuals were measured for their standard length (males: 3.8 - 6.2 cm, females: 3.5 -
164 5.1 cm) using ImageJ (Schneider et al., 2012) and transferred into individual tanks (25 cm x
165 25 cm x 50 cm) for the duration of experimental trials (5 days per individual). Tanks were
166 endowed with sand, half a clay pot as shelter and an internal filter. For identification, all
167 individuals were marked with VIEs (visible implant elastomers; VIE-Northwest Marine
168 Technology, Shaw Island, Washington, USA). Such artificial colour marks have no influence
169 on mate choice in our population (Schuett et al., 2017).

170

171 *Experimental Outline*

172 During personality testing and mate choice trials boldness was measured as activity under
173 simulated predation risk using computer animations of a naturally sympatric occurring
174 predator, the African obscure snakehead, *Parachanna obscura*. All males (N = 48) and
175 females (N = 45) used during mate choice experiments were tested for their boldness three
176 times (day 0, day 4, day 33) in order to assess the behavioural level and consistency for all
177 individuals, and short- and long-term repeatability in the population. The first and second

178 test series of male boldness tests were integrated into mate choice trials (N = 45), allowing
179 females to observe two males expressing their natural boldness. After the observation,
180 females were allowed to choose between the two males they had just observed in a
181 standard mate choice test (see *Mate Choice Trials*). For the remaining boldness trials (third
182 series of male boldness tests and all female boldness tests) the test procedure was identical
183 to those integrated into mate choice trials to ensure equal test conditions throughout.
184
185 *Boldness Test*
186 Boldness tests were conducted in a test tank (water level 10 cm, water temperature 26 ±
187 1°C; Figure 1), which was divided into three compartments: two parallel test compartments
188 in which two individuals could be tested for their boldness at the same time and an adjacent
189 observer compartment. A one-way mirror between the observer and the test compartments
190 allowed the observer to see the test individuals but inhibited test individuals to see the
191 observer. On the other short side, test compartments faced a computer monitor (Dell,
192 UltraSharp U2412M 61 cm, 24") for the presentation of predator animations. Removable
193 opaque dividers between the test and the observer compartments as well as between the
194 test compartments and the monitor allowed visual separation during acclimation before
195 trials.
196
197 Prior to a boldness test, we introduced two same-sex individuals (for details see also *Mate*
198 *Choice Trials*) into a clear cylinder (diameter = 11 cm) each, one per test compartment (test
199 compartments were permanently visually separated from each other). An observer of the
200 opposite sex was introduced into the observer compartment being allowed to freely swim

around. An observer was always introduced (even in male and female personality tests that were not integrated into mate choice trials) because it may be possible that chemical cues were transmitted from the observer to the test compartments despite physical separation. After a 15 min acclimation, the opaque dividers were removed allowing free view of the animation (test individuals and observer) and test individuals (observer). After another 1 min the cylinders were removed and the test period of 11 min started. Trials were video-recorded from above with no human being present during trials and the test tank was surrounded with white Plexiglas to avoid disturbances. Individuals were always boldness-typed at the same time of day ± 30 min to account for potential effects of time of day and hunger level on individual activity pattern (Ariyomo et al., 2015; MacPhail et al., 2009). In each boldness test, individuals were exposed to a randomly chosen animation showing a predator specimen they had not seen before.

Predator animations (N = 4, each using another specimen) were prepared using PowerPoint© following Fischer et al. (2014). Animations displayed a still photograph of the predator swimming back and forth in front of a white background. We have validated this method: *P. pulcher* decreased their activity in response to predator animations compared to a control while no difference in response towards a live predator and the animation was found (Scherer et al., 2017).

Boldness was measured as individual activity (total distance moved; cm) from the video recordings using the tracking software Ethovision XT 11 (Noldus, Wageningen, The Netherlands). The activity was assessed for a test period of 10 min, beginning 1 min after

224 the start of the video. For all individuals the behavioural level was defined as the mean
225 activity of the first and second test series. Behavioural consistency was calculated following
226 Ioannou et al. (2016) as the absolute value of the difference in activity between the first and
227 second boldness test. We further divided the measure of Ioannou et al. (2016) by the total
228 variation in the population (range of activity within first and second boldness test). As
229 suggested by Dingemanse et al. (2009), such an index would provide a measure that is
230 standardised in relation to the population. We calculated behavioural consistency for males
231 and females separately. Values for consistency can range from 0 (high consistency) to 1
232 (low consistency).
233
234 *Mate Choice Trials*
235 Mate choice trials consisted of two parts: the above described observation and a
236 subsequent choice. During observation, the female could observe two males showing their
237 natural boldness (*see Boldness Test*). Subsequent mate choice was conducted immediately
238 after the observation in a standard dichotomous choice test, suitable to predict mate
239 preference from the amount of time spent with a male in cichlids (Dechaume-Moncharmont
240 et al., 2011; Thünken et al., 2007). The choice chamber (35 x 100 x 25 cm, water level = 10
241 cm) was separated into three compartments with the female compartment being in the
242 middle (60 x 35 x 25 cm) and a male compartment at each side (20 x 35 x 25 cm).
243
244 To begin the choice test, we transferred the female and the two males she had just observed
245 from the boldness test tank to the choice chamber. Males were randomly assigned to the
246 two male compartments. All individuals were allowed to acclimate for 10 min while being

247 visually separated from each other. Then, opaque dividers were removed and the first test
248 period of 12 min began. Thereafter, the procedure was repeated with the males switching
249 sides to take account for a potential side bias (again 10 min acclimation following 12 min
250 test period). To avoid disturbances the choice chamber was surrounded with white
251 Plexiglas and no human was present during trials. Trials were video-recorded from above.
252
253 Each female was used once during mate choice trials. The two males used in a mate choice
254 trial were matched for size (standard length difference ≤ 5%, i.e. ≤ 3 mm) and family but
255 otherwise randomly chosen. The female observer originated from a different family than
256 the males.
257
258 The association time for the two males was determined from both test periods (i.e. 20 min)
259 using Ethovision XT 11. Test periods were analysed for 10 min, starting 2 min after the start
260 of the video. The association time was defined as the time the female spent within 5 cm
261 distance to each male compartment (which corresponds to ca. one fish length; hereafter
262 "preference zone"). Female strength of preference was then quantified as the relative
263 amount of time she spent in the preference zone of the bold male (association time for the
264 bold male was divided by the association time for both males; e.g. Dugatkin, 1996;
265 Makowicz et al., 2010). For each mate choice test, the bold male was defined as the male
266 being more active during the boldness test and the shy male was defined as being the less
267 active male (mean ± SE for absolute similarity between shy and bold males: behavioural
268 level = 975.95 ± 147.81; behavioural consistency = 0.11 ± 0.02; please see *Statistical*
269 *Analyses* for calculation of similarity indices). Also, we calculated the side bias for all

females and considered a female being side-biased when she spent more than 80% of the total time spent in preference zones (both test periods) in just one zone, regardless which male was there (Poschadel et al., 2009; Schlüter et al., 1998).

Statistical Analyses

All data analyses were conducted in R 3.2.3 (R Core Team, 2015). To test for personality differences repeatability of our measure for boldness (activity under simulated predation risk) was assessed with linear mixed effect models (LMMs) using the rptR-package (Schielzeth et al., 2013). We assessed short-term repeatability (boldness test: day 0, day 4) as well as long-term repeatability (boldness test: day 4, day 33) for sexes separately with 1000 bootstrapping runs and 1000 permutations. Significance was inferred when the 95% CI did not include zero. Activity was *square root*-transformed for normality and models were fit for Gaussian error structure.

To test for a general preference for bold or shy males, we ran a LMM with female strength of preference for bold males as the response and male ID as random effect. We did not include any fixed effects. To check for a deviation from random choice (i.e. strength of preference = 50%) we obtained the 95% CI of the estimated mean. A preference for either bold or shy males would be indicated if the CI does not include 0.50. Similarly, we tested for a general preference for behavioural consistency by running a null model with female strength of preference for the male showing the higher consistency during the observation as the response and male ID as random effect. A preference for either consistency or inconsistency would be revealed if the 95% CI of the mean does not include 0.50.

To test for (dis)-assortative female mate choice we fitted a LMM with female strength of preference for bold males as the response variable and male ID as random term. As fixed effects we included relative similarity for the behavioural level and relative similarity for the behavioural consistency between the female and the males she saw during the observation phase and mate choice test. To calculate relative similarity (for level and consistency, respectively), we first computed difference-score based similarity between the female and each of the two males (bold and shy) as the absolute value of the difference in the respective behaviour (e.g. Gaunt, 2006; Luo et al., 2005; Montiglio et al., 2016) between the female and the bold male, and the female and the shy male. Thus, similarity (in level and consistency, respectively) is highest at zero and dis-similarity increases with increasing values. Relative similarity was then calculated following Gasparini et al. (2015): the similarity between the female and the bold male was subtracted from the similarity between the female and the shy male. Positive values for relative similarity (in level and consistency, respectively) indicate higher similarity between the female and the bold male while negative values indicate the shy male is more similar to the female than the bold male. Prior to the analysis, we *z*-transformed both relative similarity for the behavioural level and for the behavioural consistency for standardisation.

We used the *lme4*-package (Bates et al., 2015) for LMMs. We used stepwise backward model simplification to fit the minimum adequate model. Partial R^2 with CL (confidence level) were calculated for explanatory variables using the approach suggested by Nakagawa et al. (2013), implemented in the r2glmm-package (Jaeger, 2016). For non-significant

316 explanatory variables we reported regression estimates and partial R^2 of the model before
317 the term was dropped. Model assumptions were visually ensured through model diagnosis
318 plots. For all analyses, female strength of preference was *arcsine-square root* -transformed
319 for normality. We had *a priori* decided to exclude side-biased females (N = 6) from
320 preference analyses (Dosen et al., 2004; Hoysak et al., 2007; Kniel et al., 2015; Schlupp et al.,
321 1999; Schlüter et al., 1998; Williams et al., 2010). By definition, a side-biased female shows
322 contradictory preferences during the two test periods of a choice test. The removal of such
323 inconsistent behaviour that appears random in regard to the presented males is crucial as
324 to remove females that would not express a mating preference for the presented males but
325 rather a preference for (or against) a specific side of the choice chamber (e.g. because of a
326 lack of motivation). Leaving such biased preference data in the data set would artificially
327 increase the sample size and distort the actual preference pattern. On the other hand,
328 removing side-biased females from the data set can lower the behavioural range
329 represented in this study. As there are different approaches but no common agreement in
330 how to handle side biases in mate choice trials, we performed all preference analyses twice,
331 once with and once without removing side-biased females (N = 45). Though we here
332 consider both approaches, we advocate the removal of clearly biased preference data from
333 analyses and will therefore mainly focus on the presentation of preference analyses
334 performed without obvious side biases in the data.
335
336 RESULTS
337

Males and females were significantly repeatable in their boldness over the short-term (LMM males: R = 0.507, SE = 0.110, CI = [0.246, 0.686], *N* = 48; LMM females: R = 0. 604, SE = 0. 097, CI = [0.380, 0.763], N = 45) and long-term (LMM males: R = 0. 463, SE = 0. 113, CI = [0.233, 0.657], *N* = 48; LMM females: R = 0. 557, SE = 0. 111, CI = [0.311, 0.732], *N* = 42).

We found no general preference for either bold or shy males (mean preference for bold males: 46.5 %; 95 % CI = [40.8, 52.1 %]). Also, we did not detect a general preference for male consistency (mean preference for consistent males: 53.5 %, 95 % CI = [47.8, 58.9 %]).

Female strength of preference for the bold male significantly decreased with increasing relative similarity in the behavioural level (LMM: $\chi^2_1 = 10.572$, *N* = 39, *P* = 0.001, coefficient ± SE (standardised) = -0.091 ± 0.026; $R^2 = 0.242$, CL = [0.056, 0.475]; Figure 2a). Further, female strength of preference increased with increasing relative similarity in behavioural consistency (LMM: $\chi^2_1 = 4.528$, *N* = 39, *P* = 0.033, coefficient ± SE (standardised) = 0.058 ± 0.026; $R^2 = 0.114$, CL = [0.003, 0.341]; Figure 2b).

When performing preference analysis without the removal of side-biased females, we received similar results with regard to female strength of preference for bold males (mean preference: 46.5 %; 95 % CI = [41.5, 51.6 %]) and for consistent males (mean preference: 53.9 %; 95 % CI = [49.1, 59.1 %]) not showing a deviation from random choice. However, different to the analysis with removed side biases, relative similarity in the behavioural level tended to negatively influence female preference for bold males (LMM: $\chi^2_1 = 2.885$, *N* = 45, *P* = 0.089, coefficient ± SE (standardised) = -0.043 ± 0.034; $R^2 = 0.066$, CL = [0.001,

0.258]) and relative similarity in behavioural consistency did not affect female preference (LMM: $\chi^2_1 = 2.279$, $N = 45$, $P = 0.131$, coefficient ± SE (standardised) = 0.040 ± 0.025; $R^2 = 0.052$, CL = [0.000, 0.235]).

DISCUSSION

Both sexes of *P. pulcher* showed consistent short- and long-term personality differences for boldness. We did not detect an overall agreement in female mating preference for either male level or consistency of boldness. However, we found dis-assortative female choice for the level of boldness. Also, female preference increased with similarity in behavioural consistency, suggesting assortative choice for consistency in boldness (when side-biased females were removed).

The dis-assortative preference for the behavioural level is contradictory to the results of most other mate choice studies testing for behavioural (dis-)assortment that mainly reported assortative mating preferences (e.g. Montiglio et al., 2016; Schuett et al., 2011). At this point, we can only speculate about possible adaptive benefits of a dis-assortative preference. Behavioural dis-similarity could possibly increase within-pair behavioural and/or genetic compatibility (Schuett et al., 2010). Behavioural compatibility has primarily been discussed for biparental species when both parents perform more or less the same parental activity, for instance offspring provisioning in some birds (Royle et al., 2010). In zebra finches, *Taeniopygia guttata*, for instance, similarity in the behavioural level has been

384 shown to increase pair compatibility (e.g. Schuett et al., 2011). However, when species
385 perform various parental activities they might sometimes benefit from expressing a dis-
386 assortative mating preference, facilitating role allocation during offspring care. In *P. pulcher*,
387 parents typically divide the labour with one individual staying more with the offspring and
388 the other one defending the territory. Though sexual dimorphism in role specialisation has
389 been described for many cichlids (McKaye et al., 2008; Neil, 1984; Richter et al., 2010), sex
390 roles might not be entirely strict in the species and may rather depend on the interplay
391 between male and female personality. Itzkowitz et al. (2005) have shown that male and
392 female parent convict cichlids, *Archocentrus nigrofasciatum*, changed their defense
393 behaviour in response to the mate's body size, regardless of the sex. This result indicates
394 that parental role allocation may in some species rather depend on the mate's behaviour
395 and physiology than on the sex itself. Behavioural dis-similarity in boldness may facilitate
396 labour division with the bolder individual defending the territory and the shyer individual
397 staying with the young, regardless of the sex. Hence, dis-assortative mating for personality
398 could sometimes lead to inverted parental care roles though this has not been investigated
399 yet. Also, an increased genetic compatibility through dis-similarity could be possible if dis-
400 assortative mating leads to heterozygote offspring that are more viable (Charlesworth et al.,
401 1987; Dingemanse et al., 2004). For example, Marshall et al. (2003) showed a strong
402 correlation between individual genetic diversity and a behavioural trait, song complexity, in
403 sedge warblers, *Acrocephalus schoenobaenus*. Females chose to mate with males that
404 increased offspring genetic diversity (Marshall et al., 2003). Seddon et al. (2004) found male
405 heterozygosity to be correlated with territory size and song structure in male (but not
406 female) subdesert mesite, *Monias benschi*.

Further, we found assortative mate choice for the consistency of boldness. The few studies that have assessed the link between behavioural consistency and sexual selection found a positive relationship between consistency and reproductive success (Botero et al., 2009; Byers, 2006) and a higher reproductive success of pairs matched for behavioural consistency (Schuett et al., 2011). Schuett et al. (2011) have shown that pairs matched for consistency raised foster fledglings of better body condition, indicating the possible mechanism driving assortment for behavioural consistency might be a higher efficiency in the provision of parental care.

Clearly, our study is limited by the correlative design, not allowing to specifically address the causality underlying the preference pattern. Further examinations using behavioural manipulations are now needed to decouple boldness from potentially correlated traits that might influence mate choice, to ensure the preference pattern we found is unequivocally related to individual behaviour. Moreover, it should be mentioned that our measure for behavioural consistency derived from only two measurements. We are here facing a critical trade-off. While multiple measurements can lead to a change in behaviour caused by the number of times tested, e.g. through habituation or sensitization (Bell et al., 2009; Stamps et al., 2012), the measurement error is higher when only tested twice. In this particular study, we tested individual responses towards unfamiliar predator animations, presented in a novel situation. Our measurement for boldness would likely be affected by prior experience and familiarity with test conditions, making it difficult to receive the same nature of measure for boldness when tested multiple times. However, the strength of our study is

that females could observe male boldness directly before mate choice trials while they were hidden behind one-way glass and partitions. This way, males could express their natural behaviour without being affected by the female's presence. A decoupling of observation and choice ensured female preference not being confounded by the presence of a predator.

Conclusions

In summary, we provide suggestive evidence that sexual selection may represent a key role in the evolution of personality differences. Females showed a dis-assortative mating preference for the level of boldness and an assortative preference for the degree of behavioural consistency. Our results indicate mate choice for behavioural and/or genetic compatibility though only assessed in a correlative approach. Such a mating preference might improve parental care efficiency through facilitation of parental role allocation and/or to increase offspring fitness through genetic benefits. Noticeable, the handling of side biases significantly affected our results. While we found an effect of behavioural similarity in level and consistency when removing side biases, we could not detect such effects without removing side-biased females from the data. This discrepancy in results underlines the importance of taking the approach used into consideration when comparing the results of different mate choice studies. The handling of side biases in mate choice studies is not trivial and can largely affect experimental outcomes.

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774 FIGURES

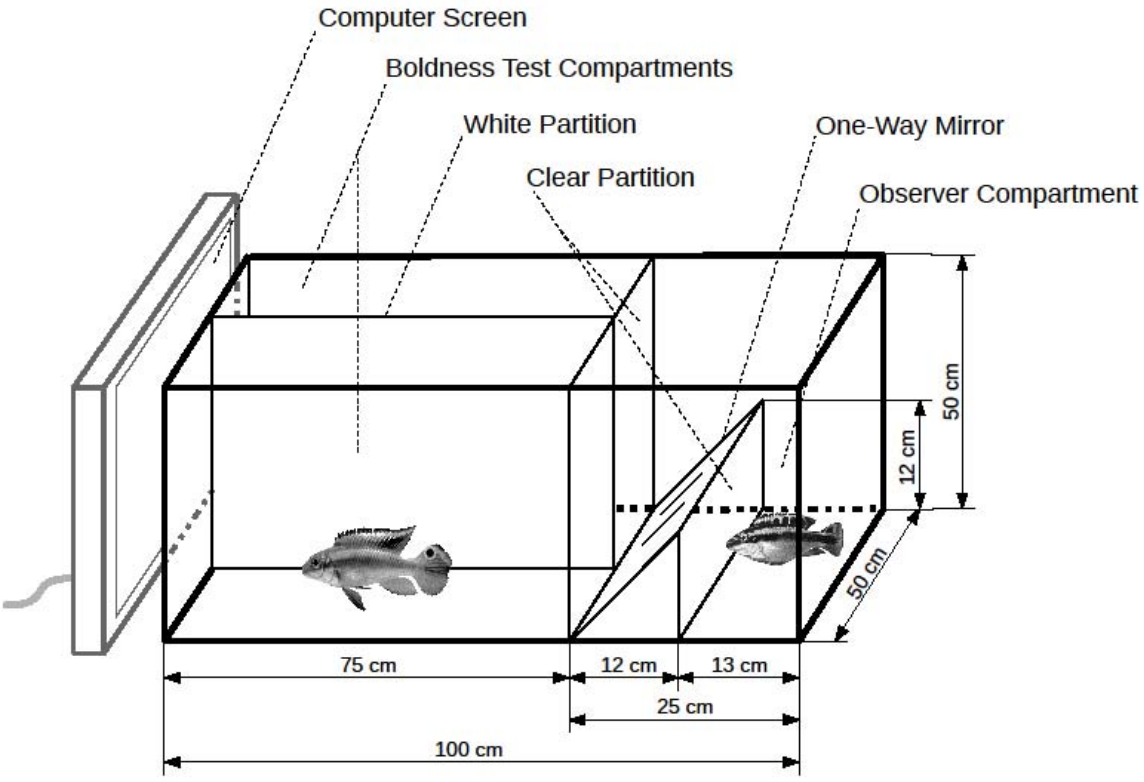

Figure 1: Experimental set-up for the boldness test. Two same-sex focal individuals (visually separated) were exposed to a video animation of a predator. Test individuals were observed by a fish of the other sex but could themselves not see the observer: the observer compartment was endowed with a one-way mirror aligned with an angle of 45° towards the test compartments providing a visual cover for the observer. Fish not to scale.

775

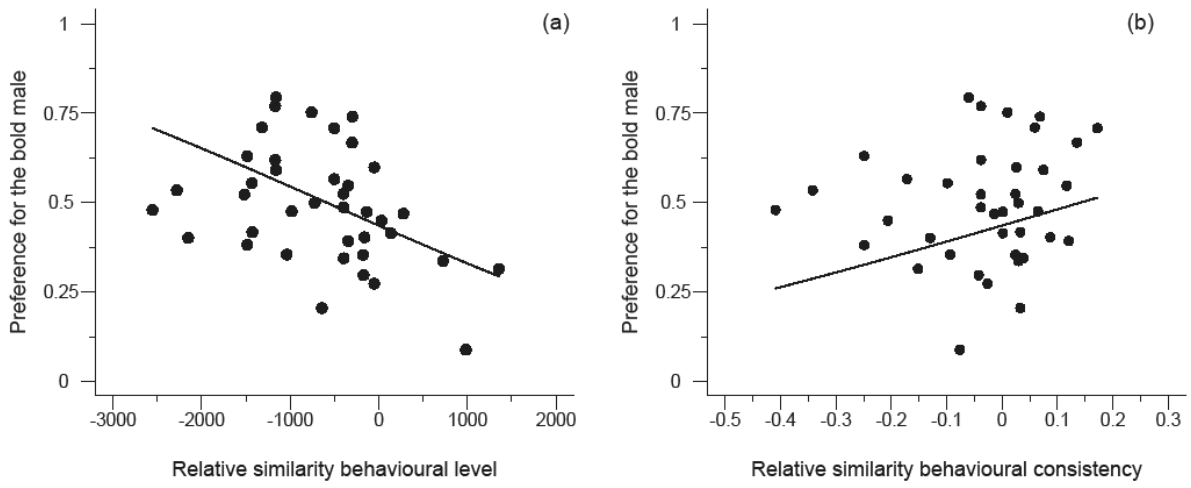

Figure 2: Female strength of preference for the bold male in dependence of relative similarity in (a) the level and (b) the consistency of boldness. Positive similarity values indicate the bold male was more similar to the female than the shy male, negative values indicate higher similarity between the female and the shy male. Data visualisation on original data, strength of preference was *arcsine-square root*-transformed for analyses.

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